Ecological Modelling 340 (2016) 45–56

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Using satellite altimetry to inform hypotheses of transport of early life stage of Patagonian toothfish on the Kerguelen Plateau

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ARTICLE INFO

Article history:
Received 15 February 2016
Received in revised form 13 May 2016
Accepted 21 August 2016
Available online 9 September 2016

Keywords:
Patagonian toothfish
Kerguelen Plateau
Recruitment
Larval transport
Connectivity
Sea surface height

ABSTRACT

Understanding patterns of oceanic transport and their role in population connectivity, particularly for the early life stages of marine organisms, has important implications for population biology and management. Various approaches have been used to observe and model larval transport and recruitment in marine environments. In the Southern Ocean, these approaches are presented with particular challenges due to logistical difficulties in accessing and sampling remote, open water or deep-sea environments. In this study, we examine the use of remotely-sensed sea surface height data (AVISO) – which is now easily accessible and available for more than 20 years – to model transport and dispersion of eggs and early larval stages of Patagonian toothfish on the Kerguelen Plateau in the Indian Sector of the Southern Ocean. We compare simulated transport patterns from AVISO with those calculated from an ocean reanalysis product (Southern Ocean State Estimate; SOSE), and draw conclusions on likely patterns of connectivity between spawning regions and regions that offer suitable habitat for juvenile fish. The results of our study suggested regions with successful spawning that are consistent with those observed by the fishery and describe inter-annual differences in simulated connectivity between spawning and recruitment habitats.

1. Introduction

1.1. The importance of understanding connectivity for early life stages of marine organisms

Understanding the lifecycle of marine species is critical to both the management of harvested species, and for evaluating and predicting ecosystem responses to environmental change. Advances in acoustic technologies, together with tagging and direct sampling have improved our understanding of recruitment processes and adult life stages for a range of species (e.g. Welsford et al., 2011; Tamdrari et al., 2012; Escobar-Flores et al., 2013; Matsumoto et al., 2013; Wall et al., 2013). However, early life cycle stages – in particular planktonic eggs and larvae – are much more difficult to observe. Survival rates at these stages can be critically important for selective pressures on particular spawning behaviours as well as spawning locations of adults that lower the risk of larvae being transported away from suitable settlement habitats (Cowen, 1985; Gaines and Roughgarden, 1987; Bradbury and Snelgrove, 2001).

Because of difficulties associated with direct observations of early life cycle stages, modelling is an effective tool for simulating patterns of larval transport in the ocean, and for evaluating factors that might influence recruitment success. A variety of modelling approaches have been used to explore transport and recruitment dynamics for marine species (e.g. Ådlandsvik et al., 2001; Brown et al., 2005; Tilburg et al., 2006; Hanchet et al., 2008; George et al., 2011; Ashford et al., 2012; Jorge et al., 2014). Here, we demonstrate the utility of satellite altimetry for modelling the advection of the eggs and early larval stages of Patagonian toothfish (*Dissostichus eleginoides*) on the Kerguelen Plateau. The lifecycle of this Southern Ocean species is poorly understood, and our study is the first to test hypotheses regarding patterns of transport and the location of spawning and recruitment habitats for Patagonian toothfish on the Kerguelen Plateau in the Indian Ocean sector of the Southern Ocean.

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http://dx.doi.org/10.1016/j.ecolmodel.2016.08.013

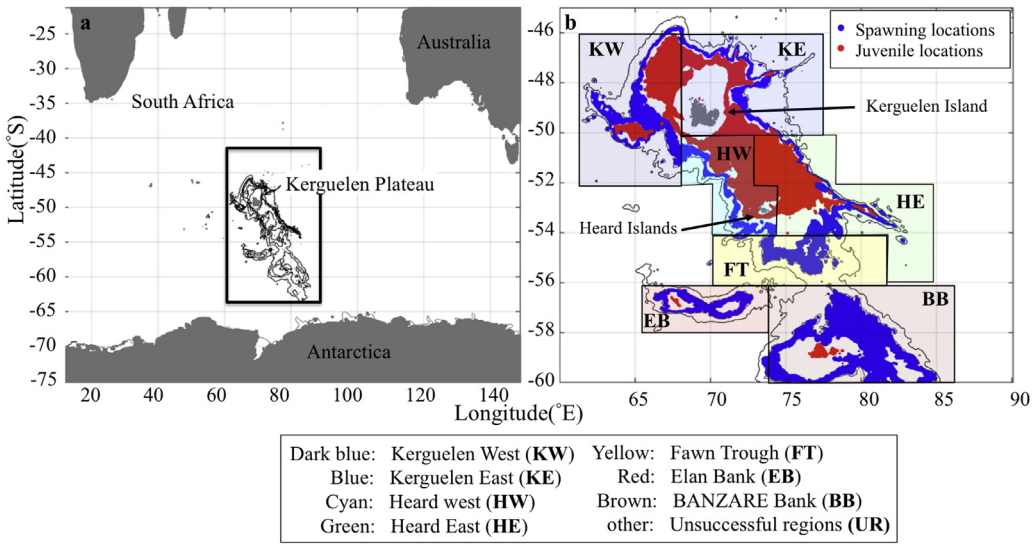

Fig. 1. (a) A map of the Kerguelen Plateau and (b) locations of interest for this study, with spawning locations (blue) and suitable habitat for juveniles (red) based on bathymetry. Coloured boxes delineate the regions used for visualizing regional-scale patterns of connectivity. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown.

1.2. Oceanography of the Kerguelen Plateau

The Kerguelen Plateau (Fig. 1) is the largest submarine plateau in the Southern Ocean; it forms a natural barrier to the Antarctic Circumpolar Current (ACC) and is a region of high productivity (van Wijk et al., 2010). When the ACC collides with the plateau it separates into smaller branches: approximately two thirds of the total transport volume is channeled to the north of Kerguelen Island and the majority of the remaining third of the transport flows through Fawn Trough that separates the northern and southern parts of the plateau. The residual current flows across the plateau between Heard and Kerguelen Islands (Park et al., 2009; van Wijk et al., 2010).

The unique bathymetry and oceanography of the Kerguelen Plateau drive high levels of primary and secondary productivity, in particular due to enhanced iron supply (Blain et al., 2007; Blain et al., 2008). Enhanced iron supply is driven by vertical mixing and high levels of retention due to relatively weak currents over the plateau itself (Park et al., 2008; Maraldi et al., 2009). Recent evidence also suggests that hydrothermal vents may provide an important, additional source of iron to support primary productivity (Tagliabue et al., 2010; Tagliabue et al., 2012). Enhanced primary productivity supports a diverse food web in this region, and the Kerguelen Plateau is an important foraging area for predators (Bailleul et al., 2010; Dragon et al., 2010).

1.3. Toothfish reproduction on the Kerguelen Plateau

The Patagonian toothfish is a demersal fish distributed around all sub-Antarctic islands and the southern tip of South America. Toothfish fisheries have a high economic value (Haywood, 2001; Lack, 2006 Collins et al., 2010) and the Kerguelen Plateau, which is situated for the most part within Australian and French exclusive economic zones and the area managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), is an important region for toothfish fisheries. Patagonian toothfish also play an important ecological role; they have a wide vertical distribution from the surface to ~2000 m depth (Evseenko et al., 1995; North, 2002; Arkhipkin and Laptikhovsky, 2010; Welsford et al., 2011; Péron et al., 2016), and at different life stages are an important prey item for seals, penguins, whales and albatrosses (Green et al., 1989; Reid 1995; Cherel et al., 1996; Charrassin et al., 2002; Lescroël et al., 2004; Purves et al., 2004; Collins et al., 2010).

The preferred habitat of toothfish varies between different life-cycle stages. Mature fish prefer deep habitats and their spawning activity occurs between 1500 m and 2000 m depth in the Kerguelen Plateau region (Péron et al., 2016). After spawning, toothfish eggs are transported upwards and early larvae and juveniles are found in the upper 200 m of the water column (Evseenko et al., 1995; North, 2002; Collins et al., 2007; Belchier and Collins, 2008; Collins et al., 2010). As fish mature, they migrate to deeper habitats (Near et al., 2003; Péron et al., 2016). On the Kerguelen Plateau, Welsford et al. (2011) and Duhamel et al. (2011) report that the western side of the plateau is an important spawning area, and that juvenile fish are found on the northeast section of the plateau (Duhamel and Hautecoeur, 2009). This is consistent with west-to-east currents in the region (Park et al., 2009 Sokolov and Rintoul, 2009; van Wijk et al., 2010) linking spawning and juvenile areas, however no studies have been undertaken to test this hypothesised link.

1.4. Approaches to modelling toothfish larval transport

Modelling the trajectories of toothfish eggs and early larvae can provide insights into the effects of ocean currents on patterns of connectivity, as well as potential locations for key spawning and recruitment habitats. Lagrangian particle tracking in hydrodynamic models is a common means of simulating larval transport for marine species (e.g. George et al., 2011; Ashford et al., 2012; Holliday et al., 2012; Young et al., 2014). This method of particle tracking usually requires the existence of a high-resolution hydrodynamic model of the study region covering the period of interest. Such models are a significant undertaking in their own right, especially if inter-annual variability is required, thus necessitating the existence of accurate inter-annual forcing data. If model output is not available for the region and time of interest then developing and undertaking a simulation is beyond the scope of most projects. The application of state-estimation products (e.g. Kanamitsu et al., 2002; Uppala et al., 2005), that use a range of observations to heavily constrain an ocean model, is another option. These models capture inter-annual variability but are only available for limited time periods for the Southern Ocean.

In this paper we investigate the option of deriving Lagrangian particle motion using geostrophic velocities at the ocean surface

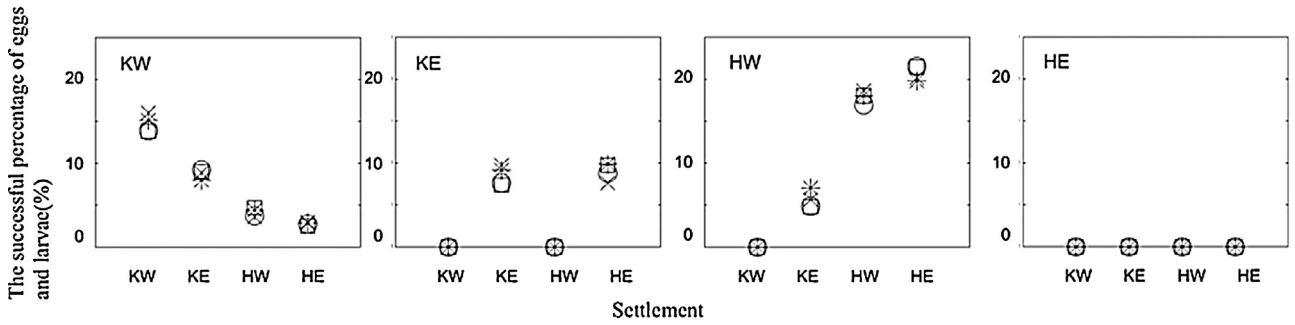

Fig. 2. Variability of successful eggs and larval transport (%) for different time steps (cross: one day, asterisk: half-day, circle; three-days, and square: one-week) from the main source regions Kerguelen West (KW), Kerguelen East (KE), Heard West (HW), and Heard East (HE) to settlement regions (x-axes) for experiment 2 in 2000.

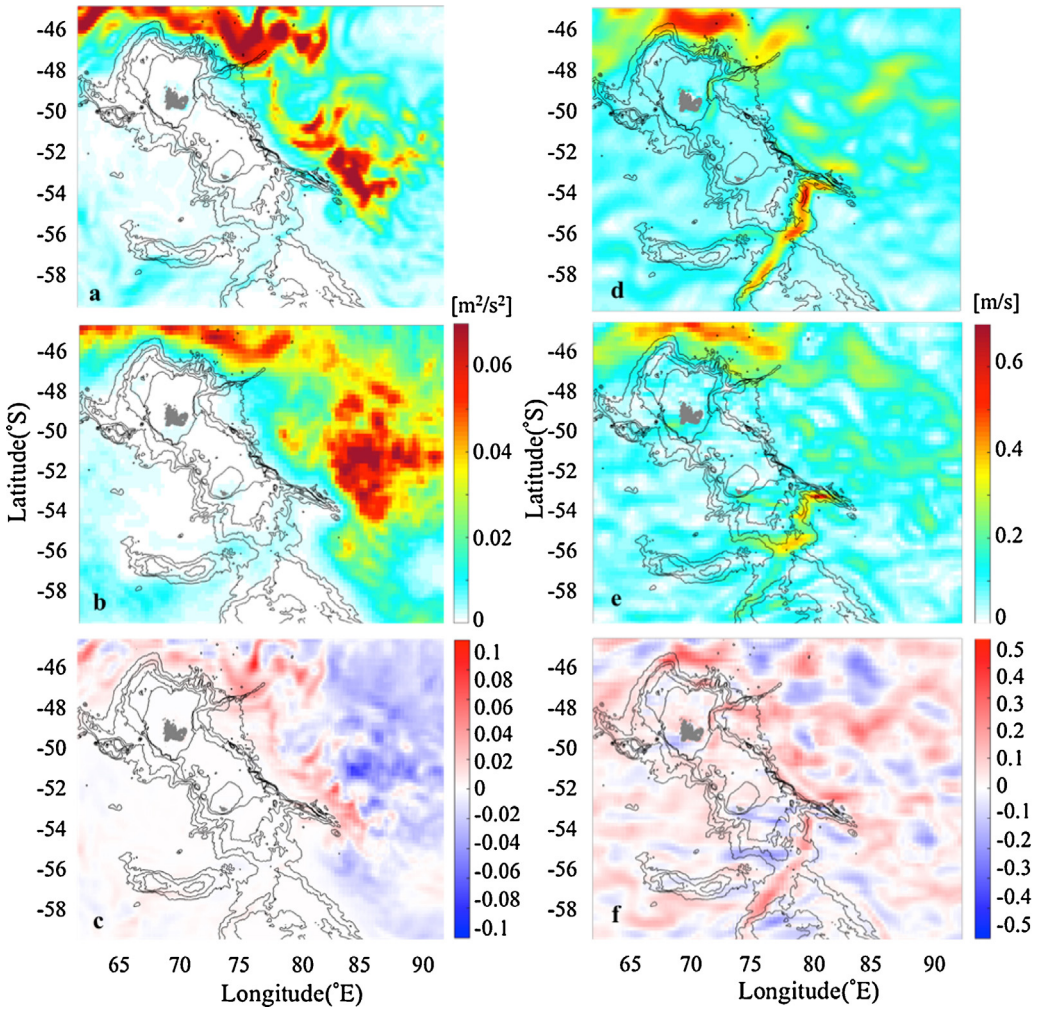

Fig. 3. Eddy kinetic energy (EKE, left) and mean flow (magnitude of velocity, right) at the ocean surface around the Kerguelen Plateau. (a) EKE from SOSE, (b) EKE from AVISO, and (c) difference between the two fields; (d) mean flow from SOSE, (e) mean flow from AVISO, and (f) difference between the two fields. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown. (For interpretation of colour in this figure, the reader is referred to the web version of this article.)

derived from satellite altimetry. Satellite altimetry has the advantages of being available at high resolution globally, ongoing and available from 1993 onwards (for example from AVISO at http://www.aviso.oceanobs.com). The use of satellite altimetry to explore patterns of connectivity for marine taxa is uncommon (Condie et al., 2005; Crochelet et al., 2013) and has not previously been attempted for the Indian Sector of the Southern Ocean.

The aims of this study are to:

- Investigate the use of satellite derived surface geostrophic velocities to explore the movement of Patagonian toothfish eggs and larvae around the Kerguelen Plateau.
- Compare patterns of connectivity predicted from satellite altimetry (AVISO) and from an ocean state estimate (SOSE).
- Investigate levels of variability in connectivity patterns across multiple years and how this may contribute to variability in recruitment success.

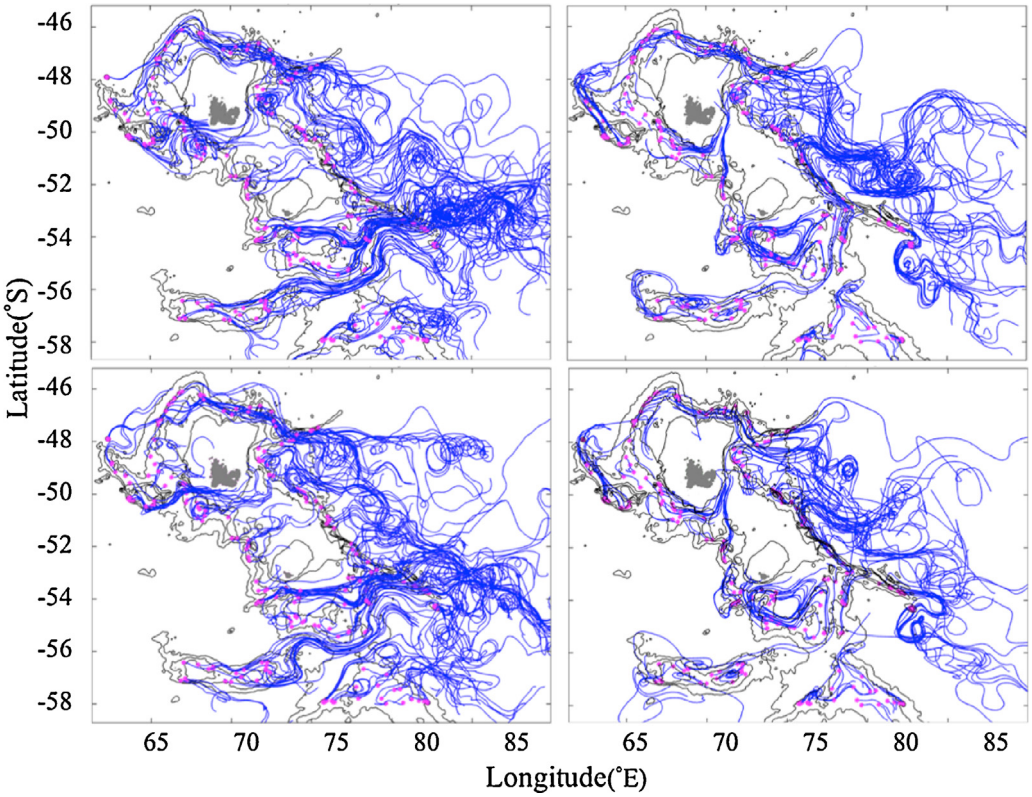

Fig. 4. Random selection of simulated trajectories from experiment 1 using velocity fields from AVISO (left) and SOSE (right) for 2005 (upper panels) and 2006 (lower panels). Asterisks indicate the randomly selected starting locations from all spawning areas on the plateau. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown.

2. Methods

2.1. Data sources

Previous studies (Duhamel, 1987; North, 2002; Collins et al., 2010) on the early development of toothfish suggest eggs and larvae are planktonic and subject to transport by currents around the Kerguelen Plateau for a period of approximately 4 months. Peak spawning for toothfish occurs in June-August each year (Duhamel, 1987; Welsford et al., 2012) and thus we chose to concentrate on the four-month (18 week) period from 1 June to 30 September for our transport simulations.

We focused the study on a seven-year period from 2000 to 2006 during which estimates of year class strength (YCS) from a stock assessment of Patagonian toothfish at Heard and McDonald Islands indicated strong inter-annual fluctuations, despite the relative high abundance and stability of the biomass of spawning stock (SC-CAMLR, 2014), and hence we hypothesised may show contrast in transport processes and connectivity. However, we did not directly compare our simulation results with the YCS estimates from the stock assessment since the latter is likely a composite of recruitment success across many areas of the plateau and settlement and post-settlement processes are poorly understood.

The primary source of data for this are the surface geostrophic velocities derived from satellite altimetry available in the AVISO archive (http://www.aviso.oceanobs.com). Specifically, we use the geostrophic velocities derived from the gridded, delayed-time reference, merged sea-level anomaly fields (known as dt_ref_global_merged_msla_uv in AVISO nomenclature). The velocity fields are available on 1/3° Mercator grid every 7 days. Since AVISO does not calculate eddies, but rather observes movement from a satellite, we consider that the 1/3° gird resolution is sufficient. AVISO output is available from 1992 onwards, i.e. to-date there are more than 20 years of data.

As a source for velocities below the ocean surface we use output from the Southern Ocean State Estimate (SOSE, Mazloff et al., 2010), an ocean model of the Southern Ocean strongly constrained to observations (including AVISO). SOSE output can be accessed at http://sose.ucsd.edu/, with data available as 5 day means or annual means at 1/6° horizontal resolution and 42 vertical levels of varying resolution. For particle tracking we use the five-day mean output. To obtain sub-surface velocities from observations (since altimetry-derived geostrophic velocities are only available at the ocean surface) we use the mean vertical decay of horizontal velocities in SOSE to scale the AVISO surface geostrophic velocities accordingly, resulting in a crude estimate of geostrophic velocities at depth. This is based on the hypothesis of the Southern Ocean having an equivalent-barotropic structure (Killworth and Hughes, 2002), details of which are not discussed here since this vertical extrapolation has negligible results on the results of this paper. SOSE output is only available from 2005 to 2010 with only two years of overlap (2005–2006) with our study period. This relatively short time period for available model output from SOSE means that it is less suitable than AVISO for assessing inter-annual variability. Furthermore there are no immediate plans for further extending SOSE.

The bathymetry used in our experiments is the 2-min grid from ETOPO2v2 (available from http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO2/). Velocities are linearly interpolated onto this grid.

2.2. Simulating transport using Lagrangian particle tracking

For successful spawning and settlement, eggs and larvae of Patagonian toothfish must be transported from spawning areas to areas suitable for larvae to settle.

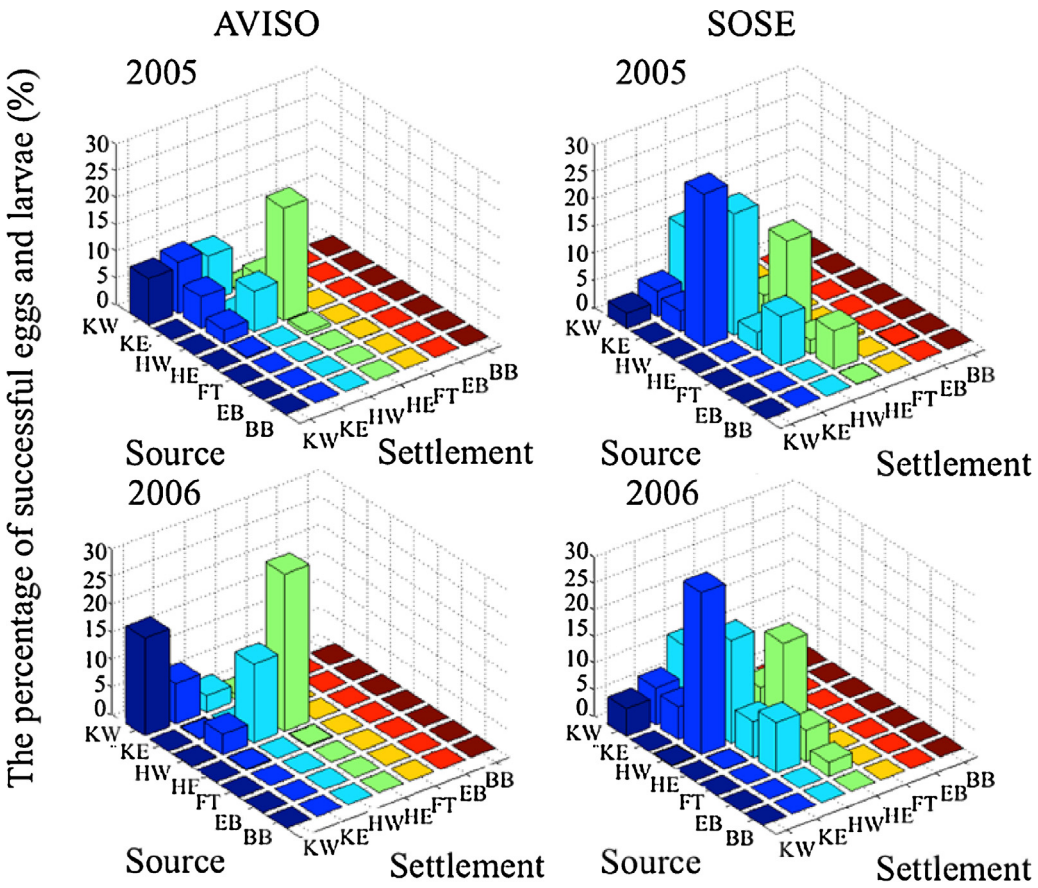

Fig. 5. The percentage of eggs and larvae that successfully reach suitable settlement regions (x-axes) when spawned in source regions (y-axes) in 2005 and 2006 from simulated trajectories using velocity fields from AVISO (left) and SOSE (right). KW is Kerguelen West, KE is Kerguelen East, HW is Heard West, HE is Heard East, FT is Fawn Trough, EB is Elan Bank, and BB is BANZARE Bank Bars are colour-coded to correspond with Fig. 1b.

Spawning areas are defined as areas with depths ranging from 1500 m to 2000 m, consistent with observations of pre-spawning Patagonian toothfish (Welsford et al., 2012). A total of 20569 points in the 2-min ETOPOv2 grid lie within this depth range and were used as starting locations of spawned eggs in our study.

Juveniles are demersal and mostly found in waters shallower than 1000 m (North, 2002; Collins et al., 2010; Duhamel et al., 2011; Welsford et al., 2011). In this study, we define the target bathymetry for juveniles as regions between 200 m to 1000 m depth, noting that the small area of the Kerguelen Plateau less than 200 m in depth is likely to be subject to tidal influences and the effects of complex, shallow bathymetry, and so eggs/larvae that cross into this region are excluded from our simulations. Thus, for larval transport to be successful, eggs/larvae released in spawning regions (1500 m to 2000 m depth) must be transported to regions suitable for juveniles (200 m to 1000 m depth) at the end of the 18-week simulation period.

To simplify our analysis we divide the Kerguelen Plateau into 7 regions (Fig. 1b), each covering areas for both spawning activity and juvenile settlement. The regions are Kerguelen West (KW), Kerguelen East (KE), Heard West (HW), Heard East (HE), Fawn Trough (FT), Elan Bank (EB) and BANZARE Bank (BB). Areas outside the suitable depth range for settlement are denoted as the unsuccessful region (UR).

Vertical transport between spawning and settlement areas is determined by egg buoyancy and depth preferences of fish larvae. The buoyancy of toothfish eggs has not been determined empirically, however experiments by Tanaka (1992) indicate that eggs from temperate perciform fish species typically rise at between 0.5 and 1 mm/s. Furthermore, despite the increased viscosity of cold water in the deep Southern Ocean which would slow the ascent of eggs, Stokes' Law predicts that relatively large diameter eggs such as those of toothfish (up to 4.7 mm, Evseenko et al., 1995) would compensate for this effect. Therefore, in this study we assume that toothfish eggs ascend at a rate of at least 1 mm/s. This implies that, in the absence of vertical currents, toothfish eggs from 1500 m depth would reach the surface at around 16 days after being released. This relatively fast ascent, compared to the overall duration of the egg and larval phase (126 days), allows us to make the approximation that the eggs spend the majority of the simulation period near the surface.

Once the eggs reach the mixed layer they are likely to move up or down with the mixing of the water (they do not have an active diel vertical migration). As a consequence, we choose to model their movement at the midway depth of the mixed layer, which for the Kerguelen region in winter is ~100 m (based on data from Sallée et al., 2010). The preferred depth for early larvae is not well known, but early juveniles and larvae have mostly been caught in the upper 200 m of the water column (North, 2002). In the simulations, eggs are spawned in regions that are between 1500 m and 2000 m deep, they then rise to 100 m depth over the next 16 days, before undergoing horizontal movement as modelled using current velocities from AVISO and SOSE. Note that in order to simplify the experiments, we do not horizontally advect the eggs in the AVISO simulations during their ascent to the mixed layer in the first 16 days. We explored the impacts of this assumption and found that due to the rapid decay of horizontal velocity with depth the final

locations of eggs were unchanged whether we assumed horizontal movement during their ascent or not (results not shown).

We also considered an alternative scenario for the early stages following spawning in which toothfish eggs rise to the surface in a much more gradual manner (eggs and larvae are neutrally buoyant and vertical movement is only achieved through upwelling of the surrounding water). Simulations of egg movement under this scenario were examined using both SOSE and a simple scheme for vertical decay of AVISO surface geostrophic velocities. This scheme also uses an equally simple mechanism for the response of larvae to bathymetry. We consider this scheme to be less realistic than surface transport but results are presented in the Appendix A for completeness.

Trajectories are calculated by numerical integration of the equations

$$\frac{dx_i}{dt} = u(x_i, y_i, t)\,; \frac{dy_i}{dt} = v(x_i, y_i, t)\,,$$

where $(x_i, y_i, t)$is the position of the particle i of at time t in a spherical coordinate system in terms of longitude and latitude, and u and v are the zonal and meridional velocities, respectively. The numerical integration has been performed in a 4th/5th order Runge-Kutta formula (ode45 in Matlab). Simulations cease when particles leave the plateau and enter open ocean, or when they "run aground" (see Fig. 1b). A time step of one day has been used; the sensitivity of the choice of time steps ranging from half a day to one week has been tested and shows less than 3% variation in successful eggs and larvae (Fig. 2). The velocities are updated weekly for AVISO data and every 5 days for SOSE data, with velocities interpolated linearly in between.

2.3. Experiments

We designed two experiments that enable us to compare patterns between AVISO and SOSE, as well as the nature of variability in larval connectivity across multiple years. In *Experiment 1*, trajectories were simulated for two years (2005 and 2006) using near-surface velocities at 100 m depth from SOSE and AVISO. The near-surface velocities in AVISO were derived by scaling the surface geostrophic velocities with the mean vertical decay of velocities in SOSE (noting that this scaling actually results in negligible differences between surface and scaled velocities). *Experiment 1* is accompanied by a sensitivity analysis to assess the effects of varying the timing of larval release, where eggs were released at 2-week intervals from June 1 for four weeks.

In *Experiment 2*, trajectories were simulated for 7 years (2000–2006) using AVISO only (also at 100 m depth). This experiment was conducted to examine the inter-annual variability in settlement locations.

3. Results

3.1. Experiment 1: AVISO/SOSE comparison

At the ocean surface SOSE and AVISO show similar patterns of mean flow and eddy kinetic energy (Fig. 3a, b, d and e) which is not surprising since SOSE is strongly constrained by AVISO data. The only significant differences are in regions where the ACC flow is strongest (Fawn Trough and north of the Plateau).

Ocean currents from both SOSE and AVISO demonstrate substantial movement across the plateau and out to the open ocean on the eastern side of the plateau (Fig. 4). While the paths taken by eggs in the AVISO and SOSE simulations differ for the two years studied, the overall results from the two simulations are consistent in showing that the western side of the plateau (KW and HW) provides most of the successful eggs, and that most of the successful

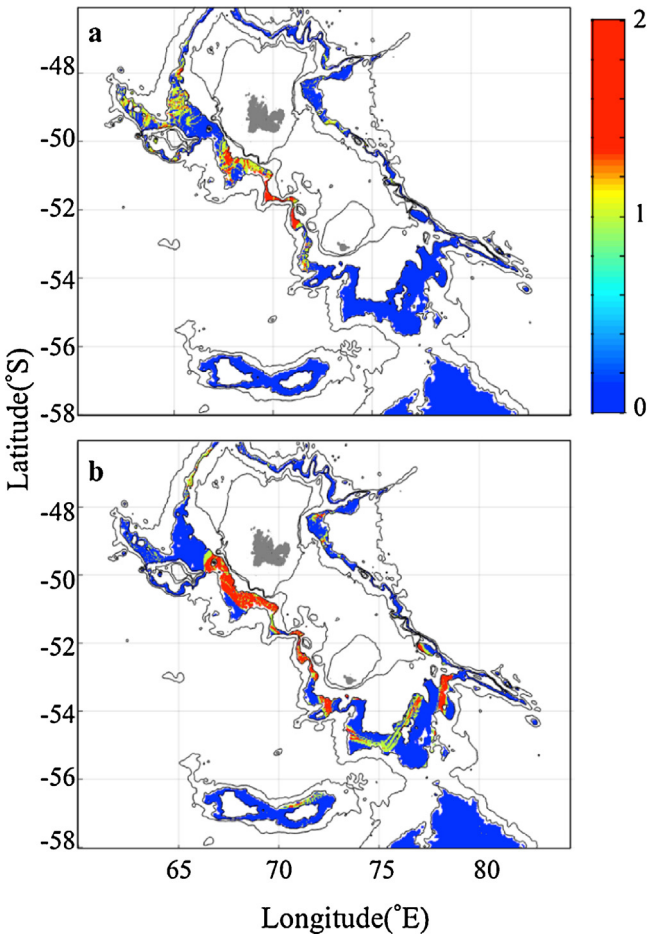

Fig. 6. Spawning locations that lead to consistent settlement success identified from experiment 1. Results are from two years (2005 and 2006) with simulations using (a) AVISO and (b) SOSE velocity fields. The frequency of successful recruitment from a particular spawning location is indicated by colour, with blue = 0, yellow-green = 1, and red = 2 out of two years. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown.

eggs spawned on the western margin end up in the eastern juvenile regions (HE and KE, Fig. 5). While eggs spawned in these eastern regions HE and KE are more likely to be transported to deep ocean areas to the east of the plateau without successful settlement in the AVISO model, the SOSE model predicted some self-retention of settling larvae for these regions.

Notable differences between the two models include higher levels of self-retention in the HW and HE regions in SOSE, a stronger south-north movement of eggs and larvae from HW to KE (Fig. 5; SOSE: above 20%, AVISO: approximately 2%), and a substantially different rate of success for eggs from Fawn Trough (FT) and Elan Bank (EB) in the southern part of the plateau. In contrast to the AVISO model, the strong current through Fawn Trough in the SOSE model (Fig. 3d) carries eggs from these two regions in north-easterly direction and into the vicinity of juvenile locations at the southern end of the Heard East region.

These differences in patterns of connectivity can be seen in the potential spawning area maps for 2005–2006 (Fig. 6). While there is consistency in successful spawning locations on the western side of the plateau, only the SOSE model indicates potential spawning locations to the south-west, south and south-east of Heard Island. The SOSE model also predicts a higher success rate in the area to the north-west of Kerguelen Island.

Sensitivity to the timing of spawning was examined by releasing eggs at two-week intervals from June 1 for four weeks (Fig. 7). The

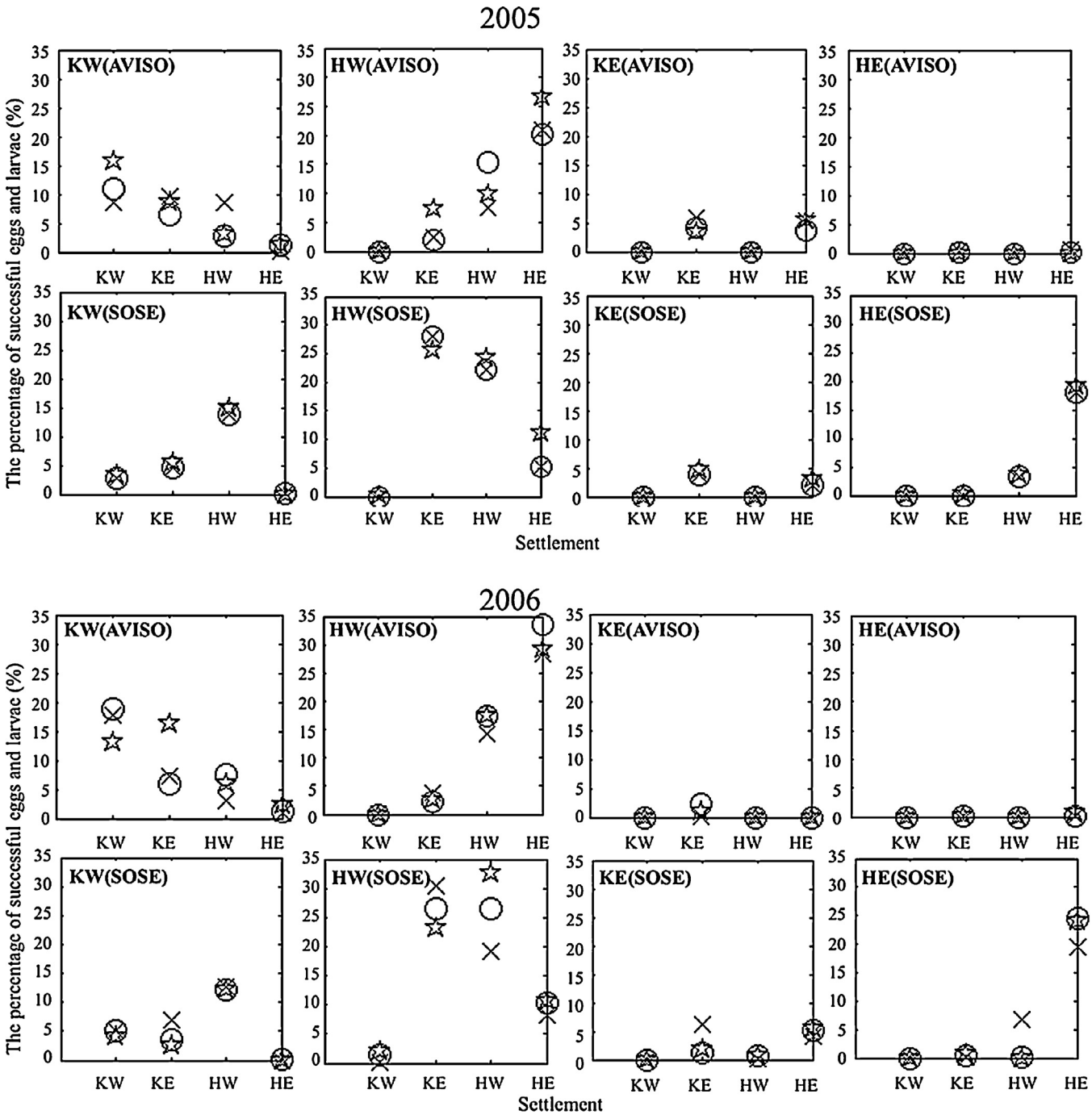

Fig. 7. Sensitivity analysis from experiment 1 for the percentage of eggs and larvae that successfully reach suitable settlement regions (x-axes) when spawned in source regions Kerguelen West (KW), Kerguelen East (KE), Heard West (HW), and Heard East (HE) for AVISO and SOSE for 2005 and 2006. Results are presented for three 18-week periods, each two weeks apart: first period (cross), second period (circle) and third period (pentagon).

analysis shows that the percentage of eggs reaching each of the four main regions is largely independent of the release date and the simulated connectivity patterns are broadly consistent across the four release dates considered.

3.2. Experiment 2: inter-annual variability

Recruitment success from spawning in the northern areas (KW, KE, HW and HE), no recruitment success from spawning in the southern areas (FT, EB and BB), and no successful exchange of recruits between the north and southern areas was consistent for the seven years of AVISO data (Fig. 8). Among the northern areas, self-retention in KW and HW showed the highest level of inter-annual variability, while their contributions to other areas were more consistent across years (Fig. 9). Kerguelen East showed some years of self-retention, while Heard East showed consistent recruitment failure.

The seven-year potential spawning area map (Fig. 10) shows the spatial distribution of locations where spawned eggs consistently reach any of the juvenile locations. The western margin of the plateau between the two islands from −51°S to −53°S is a particular hotspot for spawning success. To the north and south of this region and on the north-west tip of the plateau spawning is successful in up to five years of the simulated period. These results

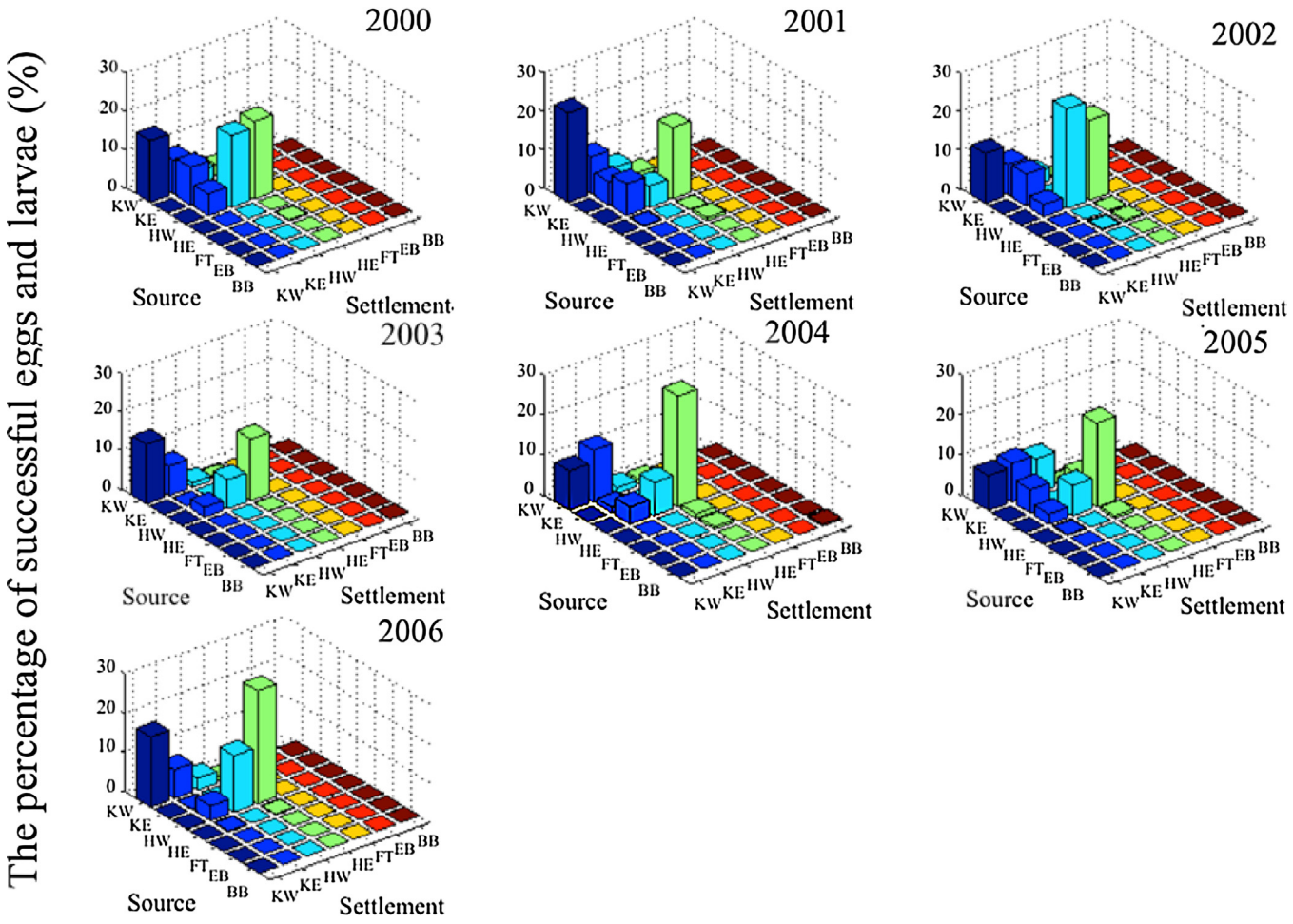

Fig. 8. The percentage of eggs and larvae that successfully reach suitable settlement regions (x-axes) when spawned in source regions (y-axes) for seven years from simulated trajectories using velocity fields from AVISO in experiment 2. KW is Kerguelen West, KE is Kerguelen East, HW is Heard West, HE is Heard East, FT is Fawn Trough, EB is Elan Bank, and BB is BANZARE Bank Bars are colour-coded to correspond with Fig. 1b.

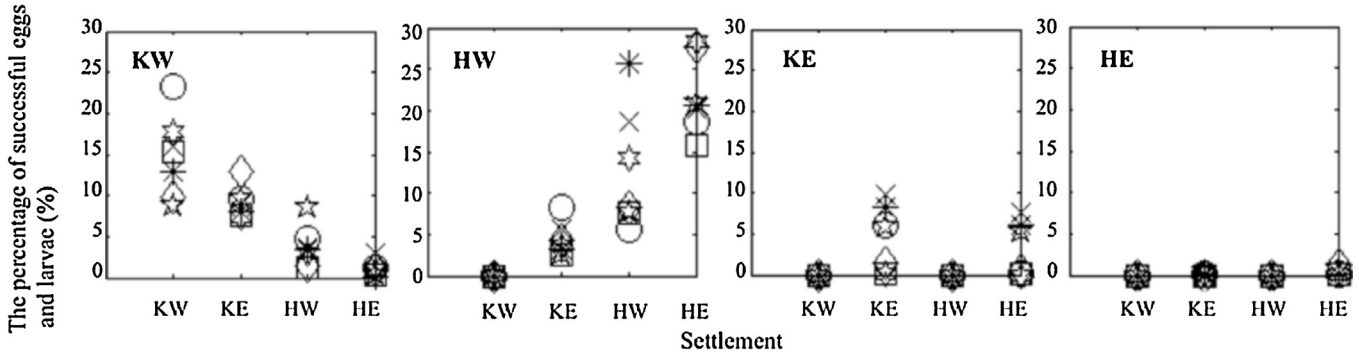

Fig. 9. Inter-annual variability in the percentage of eggs and larvae that successfully reach suitable settlement regions (x-axes) when spawned in source regions Kerguelen West (KW), Kerguelen East (KE), Heard West (HW), and Heard East (HE) from simulated trajectories using velocity fields from AVISO in experiment 2. Results are presented for seven years: 2000 (cross), 2001 (circle), 2002 (asterisk), 2003 (square), 2004 (diamond), 2005 (pentagon) and 2006 (hexagon).

suggest that inter-annual differences in currents are important for influencing the numbers of eggs that are successfully transported to juvenile locations each year.

4. Discussion

The aim of our study was to explore the feasibility of using satellite-derived geostrophic velocities in exploring patterns and connectivity of larval toothfish transport at a regional scale on the Kerguelen Plateau. For this we have used an approach of simulating ocean transport of Southern Ocean taxa that can be readily applied to determine connectivity patterns and variability across multiple years when high-resolution model output is not readily available.

Our findings suggest that satellite-derived sea surface height can provide useful indications of patterns of larval transport and connectivity when high-resolution ocean models or reanalyses are not available. The key spawning and settlement locations that we identify for Patagonian toothfish on the Kerguelen Plateau are

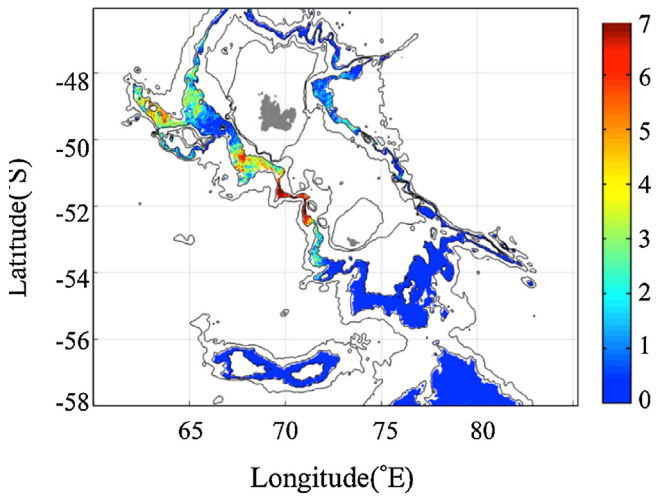

Fig. 10. Spawning locations that lead to consistent settlement success identified from experiment 2. Results are from seven years (2000–2006) with simulations using the AVISO velocity field. The frequency of successful recruitment from a particular spawning location is indicated by colour, from dark blue = 0 to dark red = 7 out of seven years. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown.

consistent with observations (Lord et al., 2006; Duhamel et al., 2011; Welsford et al., 2012; Péron et al., 2016). Welsford et al. (2012) indicate large populations of mature female toothfish concentrated on the western deep-slopes of the south part of the Kerguelen Plateau around Heard Island (Fig. 11), while Lord et al. (2006) suggests the north-western zone of plateau and around Skif Bank is a common spawning location. Péron et al. (2016) suggested that mature females are mostly found on the deep-slope regions of the plateau, while juveniles usually reside in the shallower regions on the plateau. Thus, our identified main spawning and juvenile locations are consistent with observed spawning and juvenile growing grounds. Furthermore, our results demonstrate a link between adult fish and larvae and provide a possible mechanism between observed spawning and juvenile locations. This consistency between our key result, based on our model of particle movement and previous studies based on observation can be used to improve management of toothfish fishery.

4.1. Using altimetry to model larval transport

The use of observations from satellite data such as AVISO for modelling ocean transport of Southern Ocean taxa is attractive as these datasets are comparatively small, are available for significant periods of time and directly represent geostrophic velocities.

Overall, there is a good level of correspondence in simulated patterns of connectivity between 2005 and 2006 for SOSE and AVISO. Notable difference in results from these two data sources were: (i) higher levels of self retention in the Heard West and Heard East regions in SOSE; (ii) higher levels of successful transport from Heard West to Kerguelen East in SOSE; and (iii) recruitment from Fawn Trough and Elan Bank to Heard West and Heard East in SOSE. These differences are likely to be caused by anomalies in surface currents between SOSE and AVISO and higher mean flow for SOSE over Fawn Trough and in the south-east corner of the plateau. Future work might address whether these anomalies have a consistent effect on connectivity patterns over long time periods or represent a consistent pattern.

4.2. Variability in patterns of transport and connectivity

Connectivity patterns derived from seven years of satellite altimetry from AVISO indicate that consistent recruitment success was highest for spawning areas in Kerguelen West and East, and Heard West, with high levels of self-recruitment or connectivity from western to eastern areas. These predictions, particularly for the western areas of the plateau, are consistent with field observations of large mature male and female fish to the west of Heard Island (Welsford et al., 2012; Péron et al., 2016), and the hypothesised pathway for larval transport by Welsford et al. (2011). Similarly, in the northern part of the plateau, field observations indicate that key spawning locations are located on the western side of Kerguelen Island (Lord et al., 2006; Duhamel et al., 2011) and that toothfish recruits tend to be concentrated on the eastern side of the plateau (Duhamel et al., 2011).

4.3. Next steps

We suggest three key areas of further development for this work: (i) a more realistic representation of vertical movement of eggs, (ii) some representation of larval survival to condition settlement probabilities, and (iii) evaluation of simulated trajectories and connectivity for longer time series of both sea surface height (AVISO) and state estimation (SOSE). As highlighted by Hanchet et al. (2008) in their modelling study for transport of Antarctic toothfish (*D. mawsoni*) eggs and larvae, the buoyancy and vertical movement of toothfish eggs is poorly characterized. For this reason we have assumed a simple scheme for vertical movement of Patagonian toothfish eggs with positive buoyancy transporting eggs directly to the surface. Simulations with an alternative mechanism using a very simple scheme for the response of eggs to bathymetry is presented in the Appendix, however we consider such a mechanism unrealistic.

Egg and larval mortality during transport and settlement has not been represented in this study, and percentage values for successful recruitment estimated here are likely to be overestimated. Larval transport modelling studies for other marine taxa suggest that mortality rates are not only highly uncertain, but that modelled connectivity is highly sensitive to assumptions regarding mortality (Paris et al., 2007; Houde, 2008; Gallego et al., 2012; Rochette et al., 2013). For Patagonian toothfish, availability of food for developing larvae, and predation during transport and settlement are likely to be key factors affecting recruitment success. Mortality may also vary between years and ameliorate or further extenuate the patterns of inter-annual recruitment variability predicted in this study.

While the analysis in this study was restricted to 2 years for SOSE and 7 years for AVISO, more data for both models are available and comparisons over longer time periods could provide further insights into the identification of potential key spawning locations and recruitment areas, the mixing levels of recruitment between the various areas, inter-annual variability in recruitment, and potential environmental drivers. Answers to these questions could be helpful in the management of the fisheries on the Kerguelen Plateau around Kerguelen Island, Heard Island, on Elan Bank and on BANZARE Bank, which are currently operated, assessed and managed independently.

5. Conclusion

Our study is the first to attempt to model mesoscale pelagic transport of Patagonian toothfish eggs and larvae in the Indian Sector of the Southern Ocean. It is also the first to evaluate the degree of variability in inter-annual connectivity patterns for tooth-

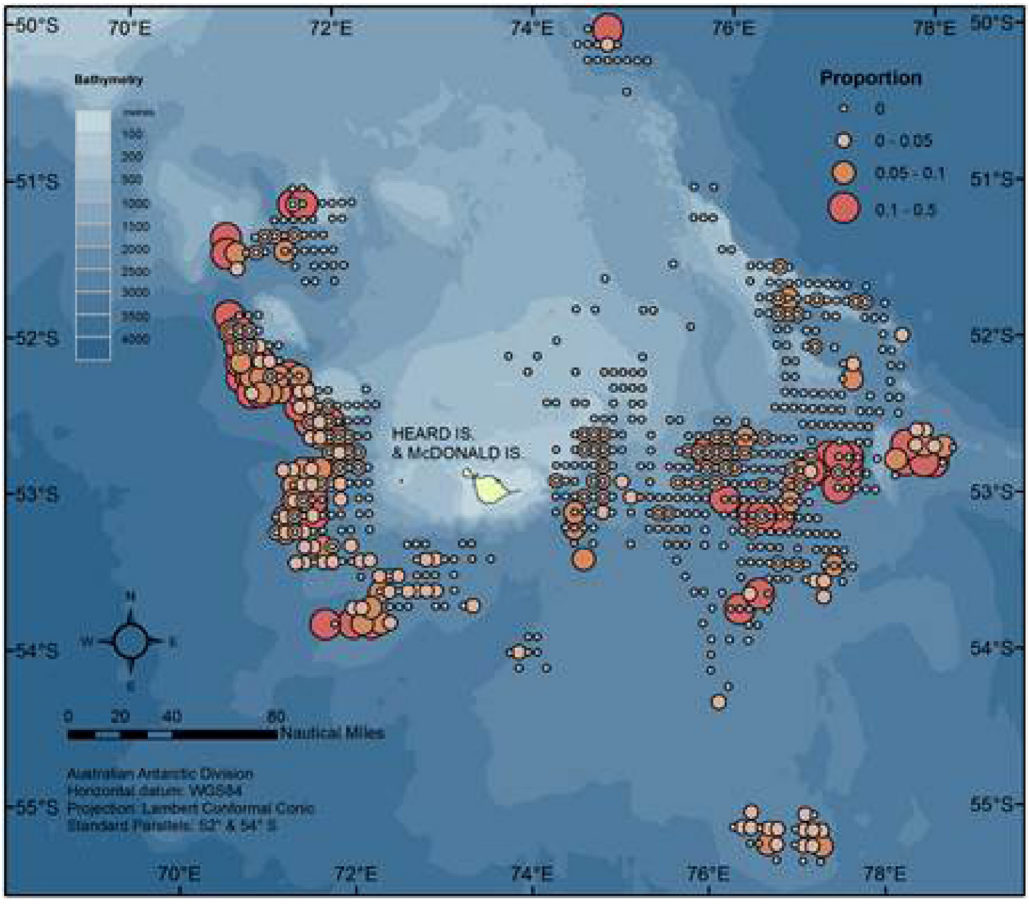

Fig. 11. Proportion of spawning female toothfish (maturity stage 3 or above) from Welsford et al. (2012).

fish species. Our results are consistent with proposed pathways for larval transport, based on observations of spawning and recruitment locations and predominant current patterns, and indicate the potential for high levels of self-recruitment, which has not previously been considered for this region. Our findings suggest that the use of satellite-derived geostrophic velocities to simulate patterns of larval transport is a promising approach that could be extended both for longer time periods and for other Southern Ocean taxa. Improved understanding of recruitment dynamics in the Southern Ocean will inform the development of management strategies for fisheries that target these species and predictions of potential responses to habitat changes in the future.

Acknowledgements

This work was supported by the Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystems Cooperative Research Centre(ACE CRC). We thank Simon Wotherspoon and Helen Phillips for helpful comments on model construction, analysis and interpretation.

Appendix A. Alternative scheme for modelling ascent of toothfish eggs and early larvae

This scheme assumes that the eggs and subsequently larvae are neutrally buoyant and vertical movement is only achieved through upwelling of the surrounding water. SOSE data provides a full three-dimensional velocity field and so the vertical component of this velocity field is able to transport larvae vertically. In contrast, the vertically extrapolated AVISO velocity field is two-dimensional and thus there is no direct mechanism for raising the eggs from spawning depths to juvenile depths.

In order to raise the eggs in AVISO simulations, we implemented a process where the eggs are raised if they are within 50 m of the seafloor. In the simulations the vertical position of eggs was evaluated each week and eggs that were within 50 m of the seafloor were raised 100 m in the water column before simulations continued. This ensured that eggs did not run aground or "tunnel" through the plateau, and is a means for approximating the vertical movement that may be caused by the presence of a barrier in the broad easterly flow.

To calculate velocities at depth from AVISO surface velocities in this scheme we followed the assumption by Killworth and Hughes (2002) that the Antarctic Circumpolar Current has an equivalent-barotropic structure, i.e. velocities at depth are in the same direction as those at the surface but at reduced magnitude. We calculated the mean vertical decay of velocities from SOSE and used this vertical decay to extrapolate AVISO geostrophic velocities in the vertical. We then compared results from this scheme with results that used SOSE three-dimensional velocity fields.

The success rate of larvae using this simulation scheme was much higher for AVISO (between 0 and 20% success) than for SOSE (99% of eggs failed to reach a juvenile location) over the two simulated years 2005–2006. This very high failure rate for SOSE is due to the small velocities at depth combined with the lack of uplift that transports the eggs to more shallow regions where horizontal velocity is larger. In contrast the AVISO trajectories are lifted towards the surface as they come close to the seafloor, thus displaying much greater movement (Fig. A1). Because of the lack of vertical movement at depth for SOSE, and the simplified scheme

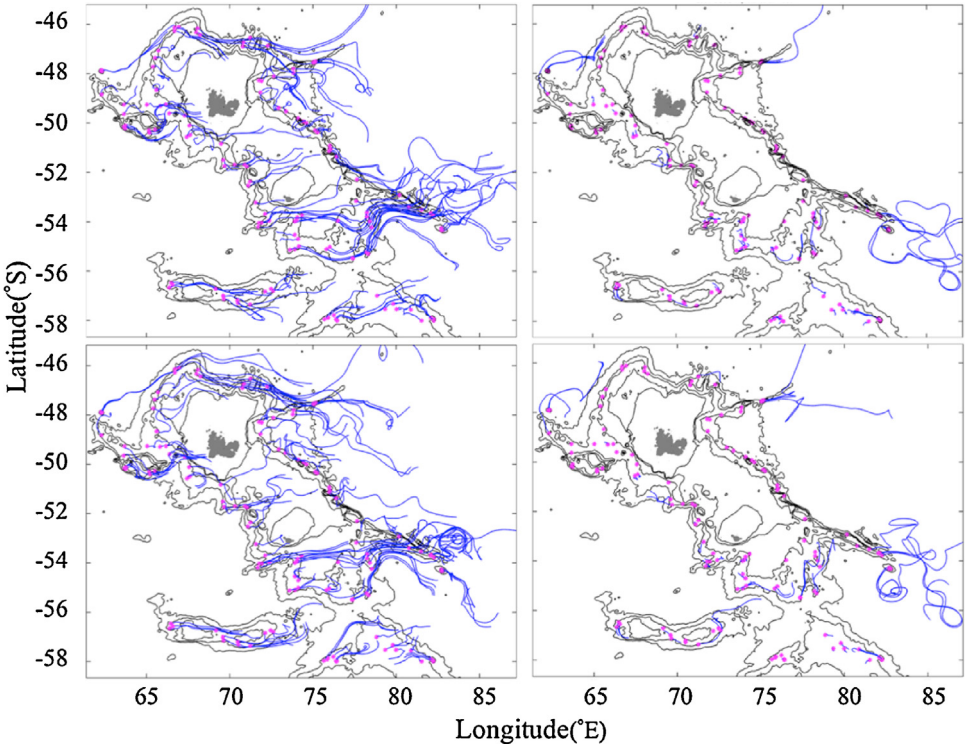

Fig. A1. Simulated trajectories assuming gradual vertical movement and using velocity fields from AVISO (left) and SOSE (right) for 2005 (upper panels) and 2006 (lower panels). Asterisks are starting locations randomly selected from all spawning areas on the plateau. The bathymetric contour lines of 400 m, 700 m, 1500 m, 2100 m and 2800 m are shown.

for vertical movement and velocity scaling for AVISO, we consider that the results from this scheme for simulating toothfish larval transport are unrealistic.

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